CHAPTER 9

Early Hominid Origins and Evolution: The Roots of Humanity

Imagine yourself walking across the hot, desolate, and altogether inhospitable landscape of East Africa's Great Rift Valley. Imagine further that you have spent the better part of the last three decades—all your adult life—searching for early hominid fossils. Over those years, you have found evidence, such as stone tools, that early humans had lived in this place hundreds of thousands—even millions—of years. Still no fossils; not even a scrap. On this particular day, you see part of a bone sticking out of the ground, just like others you have seen over and over before. This one turns out to be different, though. Instead of being an animal of some sort, this fossil has *human* teeth—you have found a hominid, your first! In an instant, all your searching has been vindicated.

That scene describes exactly what happened to the English-born anthropologist Mary Leakey (1913–1996) one sunny morning in July 1959. She, along with her husband, the Kenyan anthropologist Louis Leakey (1903–1972), had searched high and low for early human bones in Olduvai Gorge, a side branch of the Rift Valley, 50 km (31 mi) long. Since beginning their searches in the early 1930s, they had found ancient stone tools and ancient animal remains scattered about the landscape—lots of them. They wanted more, however. They wanted the remains of the people who made the tools and ate the animals. Year after year, field season after field season, disappointment after disappointment, they searched for the bones and teeth that would represent our ancestors' roots.

What had motivated these two individuals to work so hard for so little payoff under such awful conditions? Simple. They were motivated by questions. In fact, the Leakeys were asking one of the fundamental questions of all time: *Who were the first humans?* The Leakeys demanded answers about human origins, and they were willing to do what had to be done to get those answers.

They started out with a pretty simple hunch about early hominids. Other scientists had found things in Olduvai Gorge—bones and tools, both in association with really old geologic strata—that strongly suggested the place would yield early hominid remains. Based on these findings, the Leakeys decided to investigate the gorge's geologic strata (**Figure 9.1**). Their work took a lot of time and resources, but it paid off well, laying the essential groundwork for our present understanding of the first humans and their place in evolution. In fact, the bits of bone and the teeth found in 1959 turned out to be a crucially important hominid skull. Not only did this discovery expand the territory in which early hominids were known to have lived—at that point, they were known just from South Africa—but it added a whole new dimension to their variability.

The Leakeys' pioneering work in East Africa was built around questions still central to paleoanthropology.

This chapter focuses on the fossil record of early human evolution. This record sheds light on the earliest humanlike ancestors. In order of origin and evolution, they are the pre-australopithecines (before the genus *Australopithecus*), which lived 7–4 mya, and the australopithecines, which lived 4–1 mya.

BIG QUESTIONS

- What is a hominid?
- Why did hominids evolve from an apelike primate?
- Who were the first hominids?
- What was the evolutionary fate of the first hominids?

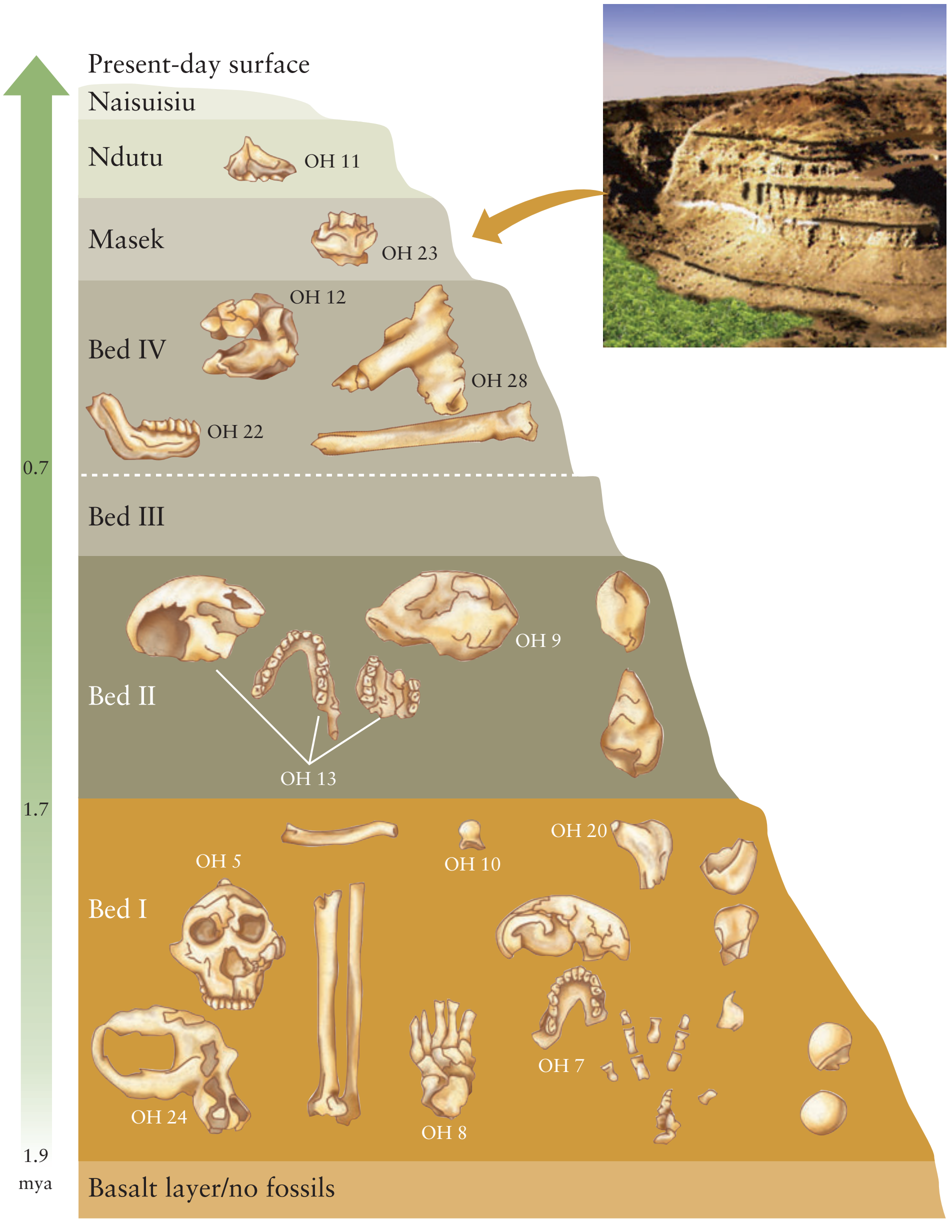


FIGURE 9.1 ■ **Geologic Strata at Olduvai** One key aspect of excavations at Olduvai is the exposed strata, dating back millions of years. The strata include volcanic rock, which can be radiometrically dated to provide accurate ages for each layer. Any fossils found in these layers can then be dated according to the stratum in which they were found. The ages of fossil hominids recovered from Olduvai Gorge help anthropologists reconstruct humans' family tree.

WHAT IS A HOMINID?

The morphological characteristics—and behaviors inferred from these characteristics—shared by living humans and their ancestors but not shared by apes reveal what is distinctive about hominids. For example, living humans speak, use language, depend fully on complex material culture, and have advanced cognition—living apes do not have these characteristics. Speech, advanced cognition, and complex material culture evolved in the human line long after the first hominids appeared in Africa, 7–6 mya, and so these characteristics do not define a hominid. Speech likely developed only in the last 2,000,000 years, and some authorities argue for late in that period. Evidence for material culture, in the form of primitive stone tools, dates to about 2.6 mya. As discussed in chapter 1, a hominid is much better understood as having two obligate behaviors—bipedal locomotion and nonhoning chewing—and the suite of associated physical characteristics that manifest these behaviors. The evidence is very clear: bipedal locomotion and nonhoning chewing preceded speech and material culture by several million years. Like large brains, speech and material culture help define humans today but were not attributes of the earliest hominids.

Bipedal Locomotion: Getting Around on Two Feet

In the 1800s, when the entire human fossil record was a very small fraction of what it is today, numerous authorities believed that the beginning of bipedalism was not the hallmark event distinguishing humans from the apes. Rather, these scientists believed that the most important initial evolutionary change was an increase in brain size, reflecting advanced (human) intelligence. They speculated that only with advanced intelligence would language, tool use, and the other behaviors that collectively define humanness have become possible. The focus on intelligence to the exclusion of other attributes helped bring about the rapid and uncritical acceptance of some purported early hominid ancestors that later turned out to be fake.

Since then, the large early hominid fossil record has proven that bipedalism—and not human intelligence—was the foundational behavior of the Hominidae, preceding most attributes associated with humans and with human behavior by *millions* of years. More than any other characteristic, the shift from walking with and running with four limbs (arms and legs) to walking with and running with two limbs (legs) distinguishes hominids from pongids (and other nonhuman primates).

Five distinguishing characteristics in the skeleton are associated with bipedalism (see also "What Is a Primate?" in chapter 6). The foramen magnum is positioned directly beneath the skull, the pelvis is short from front to back, the legs are long relative to the body trunk and arms, the foot has a double arch, and the big toe (the hallux) is not opposable. The position of the foramen magnum reflects the fact that the (bipedal) hominid carries its head atop its skull, in contrast to the (quadrupedal) ape, which carries its head on the front of the body. The shortened pelvis reflects anatomical changes that coincided with the shift from quadrupedalism to bipedalism. Especially important is the reconfiguring of the gluteal muscles for stabilizing the hip in walking on two legs (discussed in chapter 6). Bipeds have distinctively long legs, which provide the ability to stride, and to do so with minimal energy. The loss of opposability in the big toe reflects the use of this digit in helping propel the body forward during walking and running.

FIGURE 9.2 ■ **Nonhoning vs. Honing Chewing**
While humans have nonhoning chewing, primates such as gorillas (pictured here) have a honing complex, in which their very large canines cut food. The upper canines are sharpened against the lower third premolar.

Nonhoning Chewing: No Slicing, Mainly Grinding

The second of the two major differences between living apes and humans (and human ancestors), a characteristic that defines the Hominidae, is the way the dentition processes food (again, see "What Is a Primate?" in chapter 6). Apes and humans have evolved different dental characteristics, reflecting how each uses the canine and postcanine teeth (**Figure 9.2**). When apes grab onto food with their front teeth, the upper canines and lower third premolars cut and shred the food. Through evolution, apes' upper canines have become large, pointed, and projecting, with a sharp edge on the back (**Figure 9.3**). When the jaws are fully closed, each canine fits snugly in the diastema, the gap located between the canine and the third premolar on the lower jaw and the canine and second incisor on the upper jaw. The sharp edge on the back of the upper canine hones, or rubs against, a sharp edge on the front of the lower third premolar, or sectorial premolar. This honing action helps maintain a sharp, shearing edge on both the canine and the premolar. The shearing edge is essential for slicing up leaves and fruit before they are chewed by the back teeth and swallowed. Apes' lower third premolar is also distinctive in having one large, dominant cusp on the cheek side of the tooth and a tiny cusp on the tongue side of the tooth.

In contrast, living and past hominids have small, blunt, and nonprojecting canines and no diastema. Hominid canines wear on the tips instead of the backs (see Figure 9.3). The cusps on both sides of the lower third premolars are similar in size, or at least more similar in size than are apes' cusps. Unlike apes, hominids do not hone their canines as they chew.

Apes' and humans' postcanine teeth have many similar anatomical characteristics. The third and fourth premolars, upper and lower, have two cusps each. Pongids' and hominids' upper molars have four cusps, and their lower molars have five cusps. Apes' and humans' back teeth crush and slice food, with a different emphasis: humans crush food more than apes do. Apes use their molars more for slicing than crushing, reflecting their plant-heavy diet.

In apes and humans, grinding and slicing are facilitated by powerful chewing, or masticatory, muscles, especially the temporalis, masseter, and pterygoid muscles (**Figure 9.4**). Hominids place more emphasis on the front portion of these muscles, to provide greater vertical force in crushing food. Apes place more emphasis on the

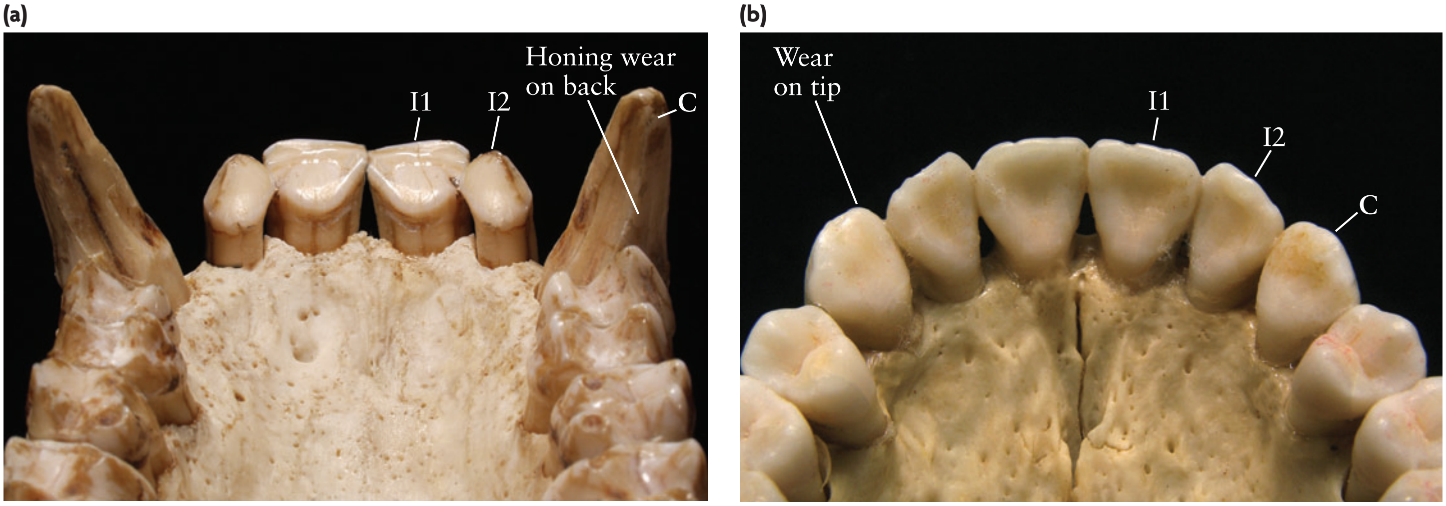


FIGURE 9.3 ■ **Canine Wear**
(a) This gorilla's dentition reveals honing wear on the back of the upper canine, caused by the tooth's rubbing against the lower first premolar. **(b)** This human's dentition reveals wear on the upper canine's tip, which is the point of contact between the upper canine and the lower teeth when the jaws are closed.

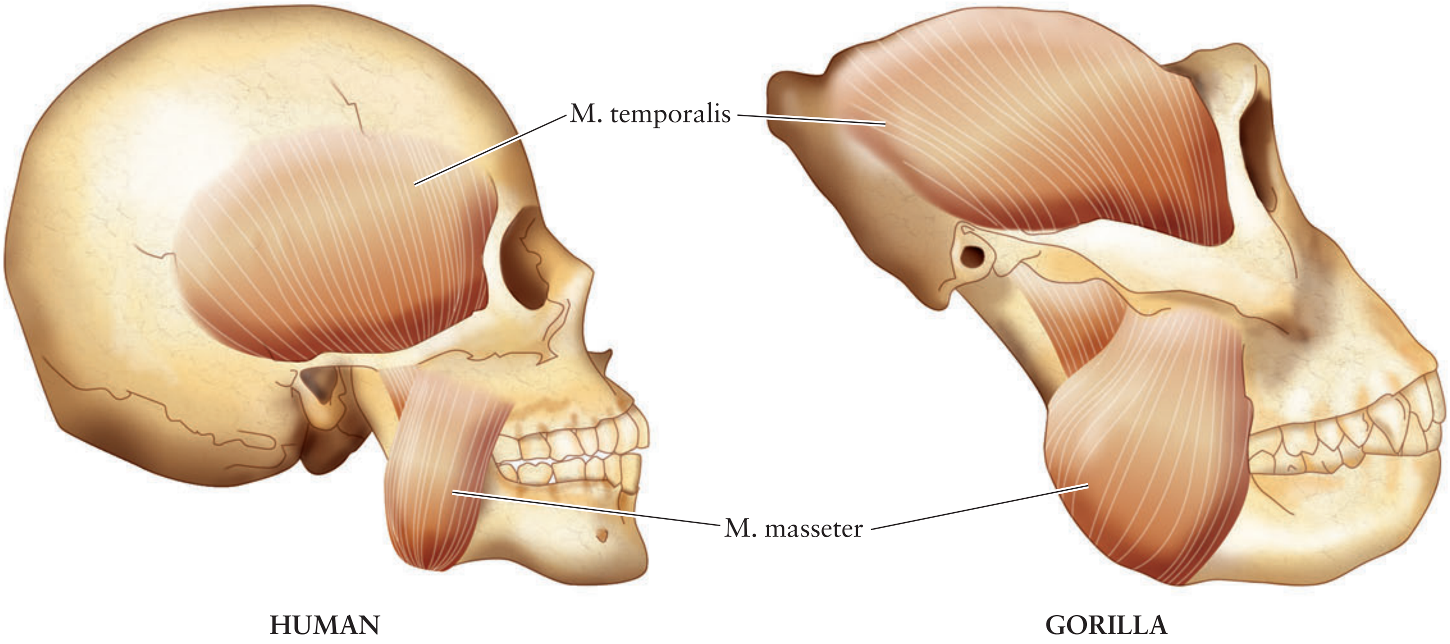


FIGURE 9.4 ■ **Masticatory Muscles**
Humans and other primates have powerful chewing muscles to process food. In humans, the temporalis muscle is vertically oriented, enabling a crushing ability. In nonhuman primates, this muscle is oriented horizontally, producing slicing motions.

back portion of the masticatory muscles because slicing requires more horizontally oriented forces. As an additional aid in powerful crushing, hominids have evolved thick enamel on their teeth (**Figure 9.5**). Pongids have evolved thin enamel, reflecting diets dominated by plants and soft fruit. Among the hominoids, the only exception is the orangutan, which has evolved thick enamel—its diet includes tough foods that require heavy crushing.

Like bipedalism, hominids' nonhoning masticatory complex evolved very early in the evolutionary record. Collectively, then, the distinguishing features of the Hominidae are located in the anatomical complexes associated with acquiring and transporting food (locomotion) and chewing food (mastication).

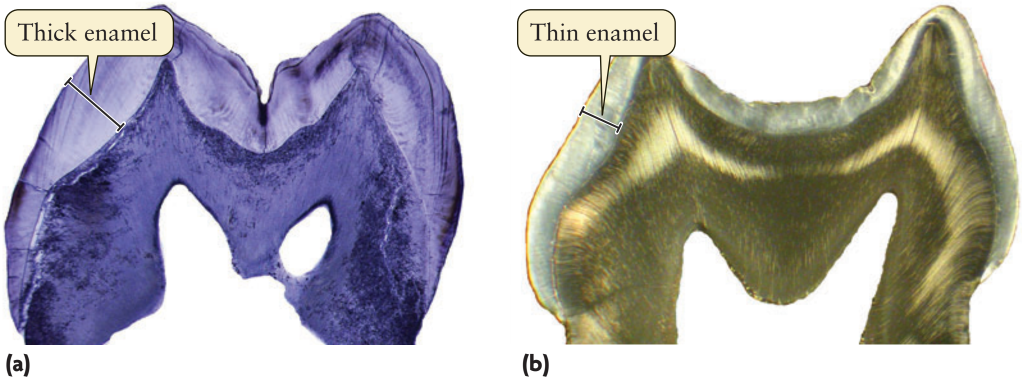


FIGURE 9.5 ■ **Enamel Thickness**
Enamel is the outermost layer of the exposed part of a tooth and is the hardest substance in the human body, enabling the tooth to grind and slice all types of food. Species with diets heavy in hard foods, such as seeds and nuts, have thicker enamel, allowing more of the enamel to be eroded or worn before the softer layers underneath are exposed. In these cross sections of **(a)** a human tooth and **(b)** a chimpanzee tooth, note how much thicker the human enamel is.

CONCEPT CHECK

What Makes a Hominid a Hominid?

Hominids have a number of anatomical characteristics that reflect two fundamental behaviors: bipedal locomotion and nonhoning chewing.

BEHAVIOR	ANATOMICAL CHARACTERISTICS
Bipedalism	Foramen magnum positioned directly beneath the skull Short pelvis from front to back Long legs Double-arched foot Nonopposable big toe
Nonhoning chewing	Blunt, nonprojecting canine Small canine relative to size of other teeth No diastema Wear on tips of canines and of third premolars Cusps on lower third premolar equal size

WHY HOMINIDS?

The fossil record and genetic information gathered from it continue to fill in the story of hominids' first appearance on the scene, in the late Miocene epoch, some 5–10 mya. But *why* did hominids evolve? Central to most arguments is bipedalism, the focal point in the study of human origins.

Charles Darwin's Hunting Hypothesis

Charles Darwin offered the first serious hypothesis about the Hominidae's first appearance. It was a simple but elegant adaptive model for explaining human origins. Drawing on the great British naturalist Thomas Huxley's anatomical research on the living apes of Africa (both Darwin and Huxley are discussed in chapter 2), Darwin concluded that because of the remarkable anatomical similarity between humans and African apes, Africa was hominids' likely place of origin. The characteristics that distinguish living humans from living apes, Darwin reasoned, derive from one key evolutionary event in their common ancestor, namely the shift from life in the trees to life on the ground. He observed four characteristics that set living humans and living apes apart: (1) humans are bipedal, while apes are quadrupedal; (2) humans have tiny canines, while apes have large canines; (3) humans rely on tools in their adaptation, while apes do not; and (4) humans have big brains, while apes have small brains (**Figure 9.6**).

Building on these observations, Darwin asked what the advantages of bipedalism would be in a world where bipeds—early humans—ate mostly meat they acquired by killing animals with weapons. He concluded that bipedalism had freed the hands for carrying the weapons. To manufacture and use these tools, the early humans needed great intelligence. Once they had the tools, they did not need the big

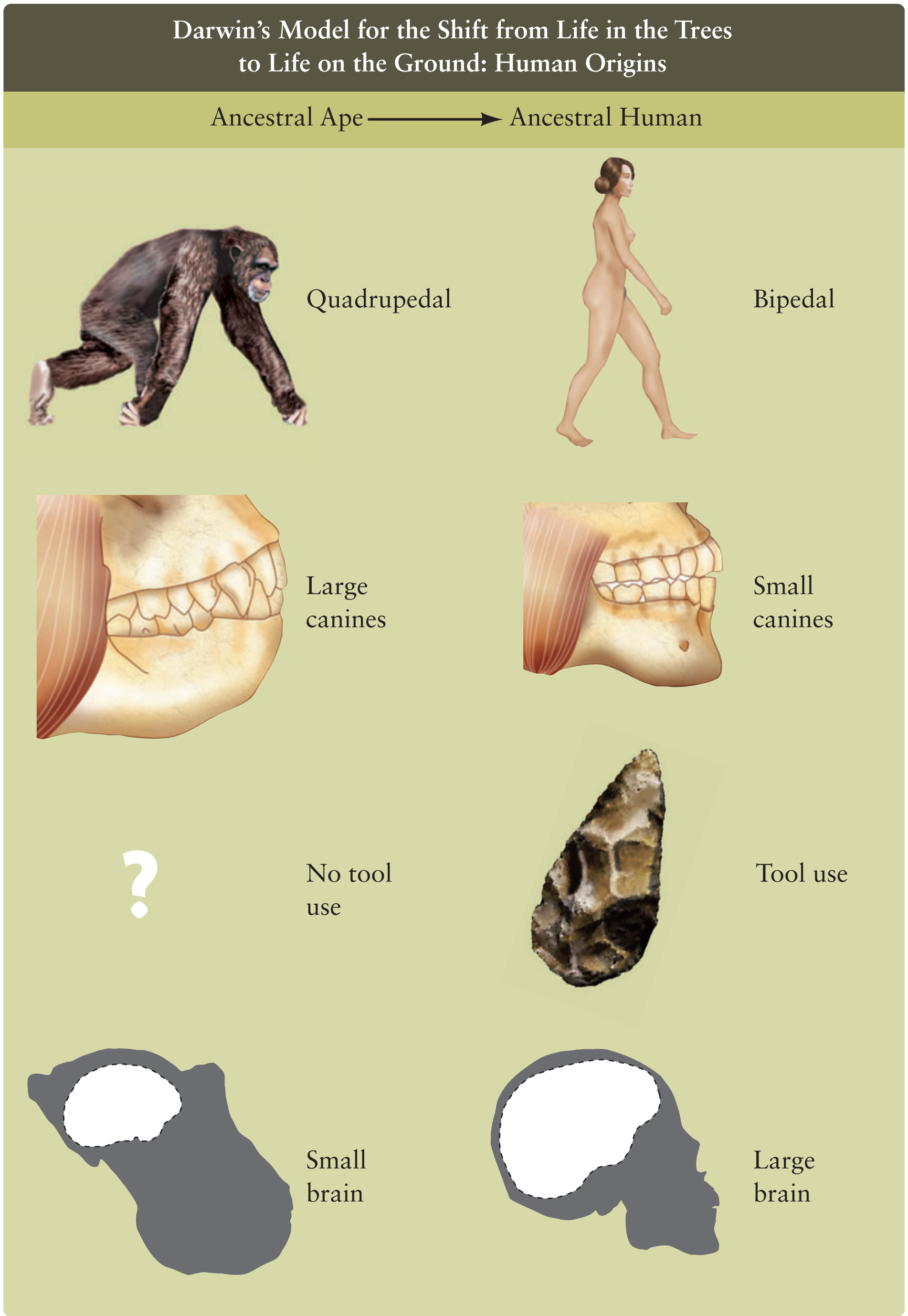


FIGURE 9.6 ■ **Four Key Differences** From Huxley's comparative studies of apes and humans, Darwin noted four differences between these two types of primates. In Darwin's time, there were no recorded instances of apes' making or using tools, so tools appeared a uniquely human phenomenon. Since then, however, apes have been seen making and using tools, such as when chimpanzees "fish" for termites with a rod and cracked hard nuts with a "hammer and anvil" (see "Acquiring Resources and Transmitting Knowledge: Got Culture?" in chapter 6).

canines for hunting or for defense. Although he saw tool production and tool use as essential factors in the development of human intelligence, Darwin believed that humans' large brain resulted mainly from the presence of language in humans.

Scientists now know that tool use and the increase in brain size began well after the appearance of bipedalism and the reduction in canine size. The earliest known tools date to about 2.6 mya, and evidence of brain expansion dates to sometime after 2 mya. Therefore, it now seems doubtful that canine reduction began with tool use. Although Darwin's hypothesis was refuted, it provided an essential first step toward an understanding of hominid origins.

Since Darwin, other hypotheses have emerged to answer the question of why there are hominids. After 17 mya, a massive adaptive diversification of apes occurred in Africa, resulting in many different taxa (see "Apes Begin in Africa and Dominate the Miocene Primate World" in chapter 8). At some point later, this diversity declined, perhaps due in part to competition between apes and to the rising number of monkey species that were also evolving in the late Miocene epoch. Changes in climate and in habitat also likely influenced the decline in the number of ape taxa. Most important about the evolution of Miocene apes is that somewhere out of this ancestral group of ape species arose the animal that was more human than ape.

Darwin proposed that hunting was at the basis of the divergence. However, the archaeological record suggests that hunting began much later in human evolution. Hunting, at least in the sense of cooperation among individuals to kill an animal, likely did not begin until after 2 mya, at about the same time the brain began expanding. It now seems likely that hunting played an important role in later human evolution but not in hominid origins.

Peter Rodman and Henry McHenry's Patchy Forest Hypothesis

The American anthropologists Peter Rodman and Henry McHenry have proposed that human origins and bipedality in particular may be related to the greater efficiency, in certain habitats, of walking on two feet rather than four feet. They suggest that bipedalism arose in areas where the forest was becoming fragmented, a process that began toward the end of the Miocene (**Figure 9.7**). Apes' quadrupedalism, they note, is not energy-efficient in Africa's patchy forests. As the forests became patchy and food became more dispersed, early hominids would have used their energy much more efficiently once bipedalism freed their hands to pick up food. The early hominids could then have fed in trees and on the ground, depending on the availability of resources.

FIGURE 9.7 ■ **East African Tree Cover**
Around the time that humans and bipedality arose, East Africa had large amounts of discontinuous tree cover. Rodman and McHenry propose that the areas of open grassland, interspersed with some stands of trees, such as shown here, favored bipedalism over quadrupedalism.

Owen Lovejoy's Provisioning Hypothesis

The American anthropologist Owen Lovejoy has offered another alternative to Darwin's ideas about the arboreal-to-terrestrial shift and the origins of bipedalism. He has hypothesized that freeing the early hominids' hands was important in initiating bipedal locomotion, but not for the reasons Darwin cited. Lovejoy observes that in many species of monkeys and apes, males compete for sexual access to females. However, the young are cared for by the mother without any involvement of the father (see "What Is a Primate?" in chapter 6). Owing to the obligations of caregiving, such as the acquisition of food for her infant (and herself), the mother theoretically is not able to care for more than one infant at a time. Moreover, she is unreceptive to mating until the infant is able to find food on its own. In apes as in humans, the time from birth to the infant's independence can be rather long, upward of five years in chimpanzees, for example. The downside of this extended care period is that it gives apes a reproductive disadvantage, since so few offspring can be born to any female. Lovejoy hypothesizes that if infants and mothers were provided with more food, they would not have to move around as much for resources. If males provisioned mothers and their offspring, each mother, again theoretically, would be able to care for two or more infants at a time. In other words, the mother could have more births—the time between births would be reduced.

Lovejoy makes the case that, for early hominids, a monogamous father enhanced the survival of the mother and her offspring by providing both food and protection from predators. This habitual provisioning required the male to have free hands for carrying food, and so bipedalism arose. This model focuses on the selective and simultaneous advantages of monogamy and of pair bonding, of food provisioning, of cooperation, and of bipedalism, all rolled into one distinctively human behavioral package.

Sexual Dimorphism and Human Behavior

Among all the hypotheses about hominid origins, Lovejoy's hypothesis had a unique focus, on differences in female and male body sizes and on the implications of behavior with a decidedly human bent. Through field and laboratory studies, anthropologists have observed that, in terms of body size, many living primate species are highly dimorphic sexually: males are considerably larger than females. This difference has come about because the larger the male, the more equipped it will be to outcompete other males for sexual access to females. Through natural selection, then, males in many primate species have maintained relatively large bodies. Some authorities argue that early hominids were highly dimorphic, in which case competing males were likely not involved in caring for their offspring. However, if early hominids were not especially dimorphic, then male competition for mates probably was not part of early hominid social behavior. The American anthropologist Philip Reno and his associates have studied early hominid bones to determine relative sizes of females and of males. Their analysis shows relatively little sexual dimorphism in body size. Such a low level of sexual dimorphism suggests that males were cooperative, not competitive. This cooperative behavior could have included pair bonding—one male paired with one female—a behavior pattern necessary for the kind of provisioning required in Lovejoy's hypothesis.

Bipedality Had Its Benefits and Costs: An Evolutionary Trade-Off

All the hypotheses about human origins have suggested that an apelike primate evolved into an early hominid through completely positive adaptation. Bipedalism's advantages over quadrupedalism included an increased ability to see greater distances (thanks to an upright posture), greater ease of transporting both food and children, ability to run long distances, and the freeing of the hands for, eventually, such remarkable skills and activities as tool manufacture and tool use. However, the profound adaptive shift to bipedalism had its costs. Standing upright yields a better view across the landscape, but it also brings exposure to predators. Standing or walking on two feet while simultaneously lifting or carrying heavy objects over long periods of time causes back injury, such as that associated with arthritis and with slipped intervertebral disks. Bipedality also places an enormous burden on the circulatory system as it moves blood from the legs to the heart. The result of this

burden is the development of varicose veins, a condition in which overwork causes the veins to bulge. Lastly, if one of a biped's two feet is injured, then that biped's ability to walk can be severely reduced. Unable to move about the landscape, an early hominid would have had limited chances of surviving and of reproducing. In short, bipedality is a wonderful example of the trade-offs that occur in evolution. Only rarely do adaptive shifts, including one of the most fundamental human behaviors, come without some cost.

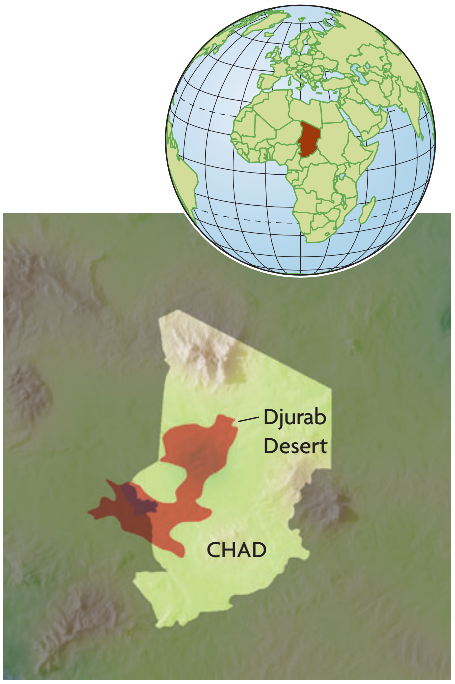
WHO WERE THE FIRST HOMINIDS?

Until a few years ago, the oldest hominid fossil dated to less than 4 mya. The earliest hominids were known from one genus, *Australopithecus,* found mostly in two key areas of Africa: a series of limestone caves in South Africa and in sedimentary basins and associated river drainages in the Eastern Rift Valley (part of the Great Rift Valley) in Ethiopia, Kenya, and Tanzania (**Figure 9.8**). As we saw in the previous chapter, the latest African Miocene apes—the group of hominoids out of which the first hominids evolved—date to about 8 mya. Thus, the crucial time period during which hominids and the last common ancestor with apes (chimpanzees) split into separate lineages has been an unknown because of the 4,000,000-year gap in the fossil record (8–4 mya). In the last few years, however, hominids predating *Australopithecus* have been discovered in north-central and eastern Africa. These hominids have closed the gap between late Miocene ape evolution and the first hominids, the pre-australopithecines.

Sahelanthropus tchadensis The earliest pre-australopithecine species found in central Africa with possible evidence of bipedalism.

The Pre-Australopithecines

Pre-australopithecine fossils are few in number and quite fragmentary, but they have provided critically important information about the origins and earliest evolution of the Hominidae. The pre-australopithecines had a number of primitive attributes, and in some respects they were more apelike than humanlike. They represent the first recognizable ancestors of the lineage leading to humans.



SAHELANTHROPUS TCHADENSIS* (7–6 MYA)** The earliest pre-australopithecine is represented by most of a skull and other fossils found in central Africa, beginning in 2001, by the French paleontologist Michel Brunet and his colleagues (**Figure 9.9**). Named ***Sahelanthropus tchadensis (meaning "genus named for the region of the southern Sahara desert known as the Sahel") by its discoverers, this creature's fossils date to 7–6 mya. The finding's geographic location—the Toros-Menalla locality of the Djurab Desert, in Chad—surprised many, because it was 2,500 km (1,600 mi) from the Eastern Rift Valley, where all other early hominids in East Africa had been found for the last three-quarters of a century. The presence of early hominids in central Africa opens a third geographic "window" onto their evolution, the first two being later presences in East Africa and South Africa. In short, humans originated in Africa during the late Miocene and early Pliocene.

Cranial capacity, a rough measure of brain volume, is one important quantitative characteristic with which anthropologists determine the degree of humanness in individual fossil hominids. The fossil record of human evolution shows an increase in brain size, from the smallest in the oldest hominids (about 350 cubic

FIGURE 9.8 ■ **African Hominids**
Many hominid fossils have been found in East Africa and South Africa.

FIGURE 9.9 ■ ***Sahelanthropus tchadensis***
Among the first and few hominid fossils uncovered in central Africa, this skull belonged to a primate with a small and primitive brain like that of apes. Note the large browridge.

centimeters, or cc) to the largest in *Homo sapiens* (about 1,400 cc). *Sahelanthropus* has a brain size of about 350 cc.

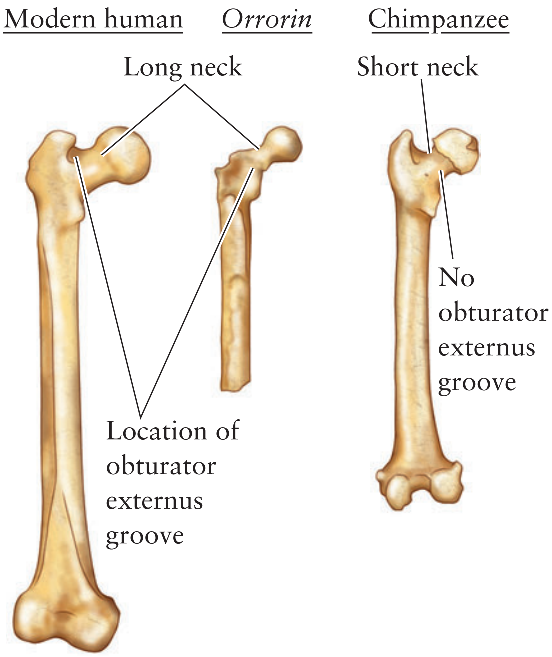
Its brain was primitive and like that of apes. Moreover, this hominid had a massive browridge, larger than that of modern gorillas. However, the two critical attributes that define the Hominidae are present in *Sahelanthropus*—the primate was likely bipedal (based on the position of the foramen magnum at the base of the skull) and the canine-premolar chewing complex was nonhoning. This combination of primitive (more apelike) and derived (more humanlike) features is to be expected in the oldest hominid, especially in apes' and humans' common ancestor. Its great age and primitive characteristics indicate that *Sahelanthropus* existed very close—the closest of any fossil known—to the divergence of their common ancestor into pongids and hominids.

Also found at the same site were the bones and teeth of nonprimate animals, fossils that create a picture of *Sahelanthropus*'s habitat. These remains—of hugely diverse animal species, including fish, crocodiles, and amphibious mammals associated with aquatic settings, and bovids (hoofed mammals), horses, elephants, primates, and rodents associated with forests and grasslands—indicate that *Sahelanthropus* lived in a forest near a lake.

ORRORIN TUGENENSIS* (6 MYA)** Dating to around 6 mya, the fossils of at least five pre-australopithecines were found in the Tugen Hills, on the western side of Kenya's Lake Turkana. The discoverers, paleoanthropologists Brigitte Senut and Martin Pickford, named these hominids ***Orrorin tugenensis (the genus means

Orrorin tugenensis A pre-australopithecine species found in East Africa that displayed some of the earliest evidence of bipedalism.

FIGURE 9.10 ■ ***Orrorin tugenensis***
The most important skeletal remain of this pre-australopithecine is a proximal, or upper, portion of the femur, which has a long femoral neck and a groove for the obturator externus muscle. These are the same as in humans and hominid ancestors, suggesting *Orrorin* was bipedal. By contrast, apes (such as the chimpanzee) have a short femoral neck and no groove.



"original man" in Tugen's local language). Among the 20 remains were several partial femurs, each missing the knee but indicating that these hominids were bipedal. For example, the femur's neck, the area that is at the top of the bone and articulates with the hip, was relatively long (**Figure 9.10**). A hand phalanx found at the site was curved like a living ape's, suggesting that *Orrorin* spent time in the trees. Like those of *Sahelanthropus,* the canines had wear on the tips and were nonhoning. The animal bones at the site indicated that *Orrorin* lived in a forest.

***ARDIPITHECUS KADABBA* AND *ARDIPITHECUS RAMIDUS* (5.8–4.4 MYA)** In Aramis, a site within the fossil-rich Awash River Valley of Ethiopia's expansive Afar Depression, the American anthropologists Tim White and Yohannes Haile-Selassie and their colleagues discovered the youngest pre-australopithecine species. The Middle Awash is an especially important place in the study of human evolution because it has yielded some of the most significant early hominid remains. Numerous pre-australopithecines, australopithecines, early members of *Homo*, and early modern *Homo sapiens* have been found in the area, providing a fabulous record of nearly continuous human evolution (**Figure 9.11**).

For a very long time, nearly 1,500,000 years, Aramis was occupied by at least two pre-australopithecines—an earlier and a later species of *Ardipithecus* known as, respectively, ***Ar. kadabba*** and ***Ar. ramidus*** (*Ardi* means "ground" or "floor" in the Afar's local language; *rama* means "root"). These pre-australopithecines date from the late Miocene (ca. 5.8 mya) to the early Pliocene (ca. 4.4 mya). The remains include a partial skeleton and other bones and teeth. The chewing in the earlier form of *Ardipithecus* (ca. 5.8–5.6 mya) was quite primitive. Although the dentition lacked functional honing, the presence of some polishing on the outside of the third lower premolar is a primitive trait consistent with its very early date (**Figure 9.12**).

The later form of *Ardipithecus* (4.4 mya) did not employ this primitive form of perihoning. Rather, its molars ground, and the tips of its canines chewed. *Ardipithecus* is unusual in being the fossil record's only hominid with thin enamel. Its curved foot phalanges reflect arboreal activity (**Figure 9.13**). Its femur and pelvic bones indicate bipedalism. *Ar. ramidus* was only about 1 m (somewhat over 4 ft) tall.

Ardipithecus kadabba An early pre-australopithecine species from the late Miocene to the early Pliocene; shows evidence of a perihoning complex, a primitive trait intermediate between apes and modern humans.

Ardipithecus ramidus A later pre-australopithecine species from the late Miocene to the early Pliocene; shows evidence of both bipedalism and arboreal activity but no indication of the primitive perihoning complex.

FIGURE 9.11 ■ **Middle Awash Valley, Ethiopia**
This hotbed of hominid fossil finds is located in the Afar Depression, an area of much geologic and tectonic activity. The Awash River flows through the depression, creating rich plant and animal life in the midst of an arid region. Because the Afar's floor consists of volcanic rock, radiometric dating methods can be used to provide age estimates for the fossils found in the geologic strata. The large amount of earthquake activity fissures the rock, allowing researchers to excavate layers that are millions of years old.

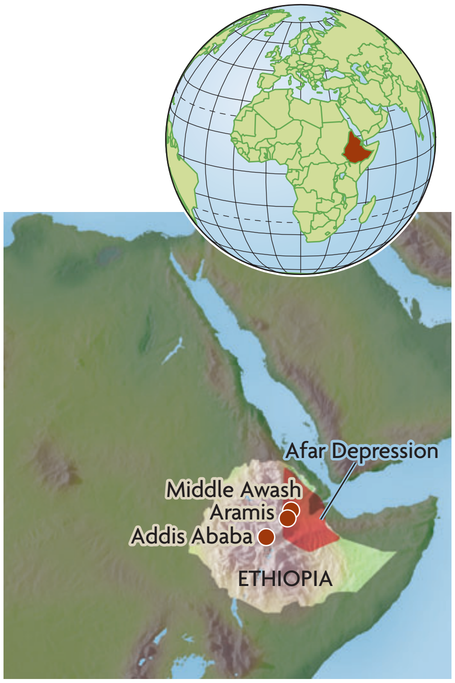


FIGURE 9.12 ■ ***Ardipithecus kadabba***
The earlier form of this pre-australopithecine had an intermediate honing, or perihoning, complex in its dentition, while the later form lacked honing entirely. Shown here, the perihoning complex of an early form of *Ardipithecus* (right) as similar to chimpanzees' honing complex (left). Together, these forms suggest that *Ardipithecus* was an early hominid ancestor, as its dental morphology was intermediate between apes' and humans'. (Photo © 2003 Tim D. White/Brill Atlanta.)

FIGURE 9.13 ■ **Foot Phalanges**
There is evidence that *Ardipithecus* was bipedal. However, its foot phalanges are curved like apes', suggesting that this pre-australopithecine was arboreal at least some of the time. Like its dentition, this anatomical evidence suggests *Ardipithecus* was an intermediate genus. (Photo © 2003 Tim D. White/Brill Atlanta.)

CONCEPT CHECK

The Pre-Australopithecines

The first hominids spanned a 3,000,000-year period in Africa, about 7–4 mya. They had both apelike characteristics and the features that define hominids.

HOMINID	DATE(S)	LOCATION
Sahelanthropus tchadensis  Key features: Skull and teeth found Tiny brain (350 cc) Skull like apes', with massive browridge Lived in forest setting	7–6 mya	Djurab Desert, Chad
Orrorin tugenensis  Key features: Postcranial bones found Femurs indicate likely bipedalism Hand phalanx like apes' (curved) Less than 1 m (4 ft) tall Lived in forest setting	6 mya	Tugen Hills, Kenya
Ardipithecus kadabba  Key features: Skull, teeth, postcranial bones found Small brain Some tooth wear on outside of third premolar (perihoning) Thin enamel Curved foot phalanges Femur and pelvis indicate full bipedalism Less than 1 m (4 ft) tall Lived in wooded setting	5.8–5.6 mya	Awash River Valley, Ethiopia
Ardipithecus ramidus  Key features: Skull, teeth, postcranial bones found Small brain No perihoning Thin enamel (only hominid with thin enamel) Curved foot phalanges Femur and pelvis indicate full bipedalism Less than 1 m (4 ft) tall Lived in wooded setting	4.4 mya	Awash River Valley, Ethiopia

Like those of *Sahelanthropus* and *Orrorin*, the Aramis fossils were found in a wooded setting, revealed by the presence of seeds, wood, and the bones and teeth of forest-dwelling monkeys and of forest-dwelling kudus. Thus, the pre-australopithecines share several key attributes: they were extraordinarily primitive, they were highly diverse, and they lived in wooded settings throughout Africa. They spent a lot of time on the ground, but also spent time in trees. The emerging picture of the first hominids as forest-dwellers calls into question the earlier notion that bipedality developed first in open grasslands. As far back as the 1800s, early hominids had been identified as having lived in a time period with a dryer climate. Bipedalism was thought to have been an adaptation to this new kind of climate and its associated open grasslands. It now seems unlikely, however, that early hominids first evolved in grasslands (**Figure 9.14**).

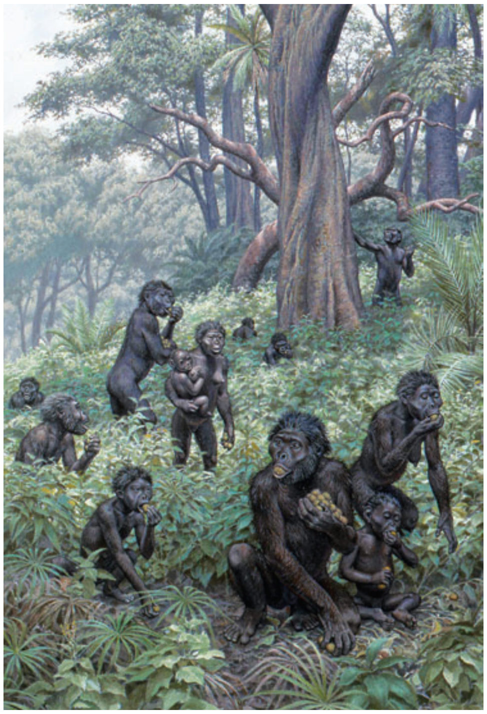


FIGURE 9.14 ■ **Origins of Bipedalism**
The earliest hominid ancestors, the pre-australopithecines, lived in a forested setting, although it might have had a discontinuous tree cover. Contrary to earlier hypotheses, bipedalism appears to have originated not in open grasslands but in an environment with trees. ("*A. afarensis* Group Gathering Figs in an Ancient Hadar Forest," © 1985 by Jay H. Matternes.)

The Australopithecines (4–1 mya)

The australopithecines are represented by hundreds of fossils of at least seven species from one genus, *Australopithecus*. Some of the species represent members of ancestral-descendant lineages (**Figure 9.15**). For the other species, however, anthropologists are sorting out the lineage relationships. Compared with other mammals, australopithecines did not vary greatly. Their variation was mostly in size and robusticity—from relatively small and gracile to large and robust. As a group, the australopithecines had a small brain, small canines, large premolars, and large molars (**Table 9.1**). The later australopithecines' face, jaws, and teeth were very large.

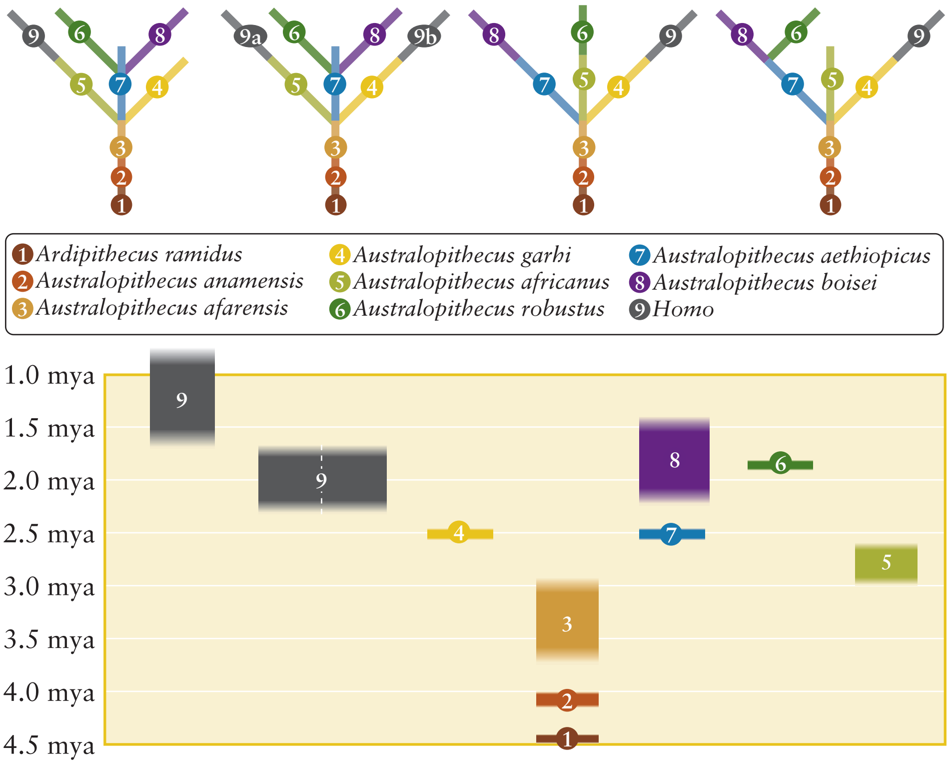


FIGURE 9.15 ■ **Hominid Phylogenies**
These four alternative phylogenies depict the possible ancestor-descendant relationships among the many australopithecine species. In each tree, *Ardipithecus* is at the base, leading to its descendant *Australopithecus anamensis,* one of the earliest australopithecines. In the second tree, the 9a and 9b indicate that the *Homo* genus may have been the product of both ancestors.

TABLE 9.1 The Earliest Hominids Evolve

	PRE-AUSTRALOPITHECINE	→	AUSTRALOPITHECINE
Teeth	Canine with modified honing	→	Nonhoning
Bones	Vestiges of apelike arboreal traits	→	Loss of traits
Brain	Small	→	Slight increase

Australopithecus anamensis The oldest species of australopithecine from East Africa and a likely ancestor to *A. afarensis*

Australopithecus afarensis An early australopithecine from East Africa that had a brain size equivalent to a modern chimpanzee's and was thought to be a direct human ancestor..

AUSTRALOPITHECUS ANAMENSIS* (4 MYA)** The oldest australopithecine species, ***Australopithecus anamensis (*anam* means "lake" in the Turkana language), was named and studied by the American paleoanthropological team of Meave Leakey, Carol Ward, and Alan Walker. *A. anamensis* dates to about 4 mya and was found within Allia Bay and Kanapoi, in, respectively, the eastern and southern ends of Lake Turkana, Kenya. Other remains, found at Asa Issie, Ethiopia, have been studied by the American anthropologist Tim White and his colleagues. This creature was broadly similar in physical appearance to *Ardipithecus,* enough to indicate a probable ancestral-descendant relationship between the two genera. Reflecting its relatively early place in australopithecine evolution, *A. anamensis* has a number of primitive, apelike characteristics, including very large canines, parallel tooth rows in the upper jaw, and a lower third premolar with both a very large outer cusp and a very small inner cusp (**Figure 9.16**). The fossils were created in woodland environments.

AUSTRALOPITHECUS AFARENSIS* (3.6–3.0 MYA)** Since the early 1970s, fossils representing ***Australopithecus afarensis have been found in two main sites: Laetoli, in Tanzania, Kenya; and Hadar, in Ethiopia (*Afar* is the name of the local tribe

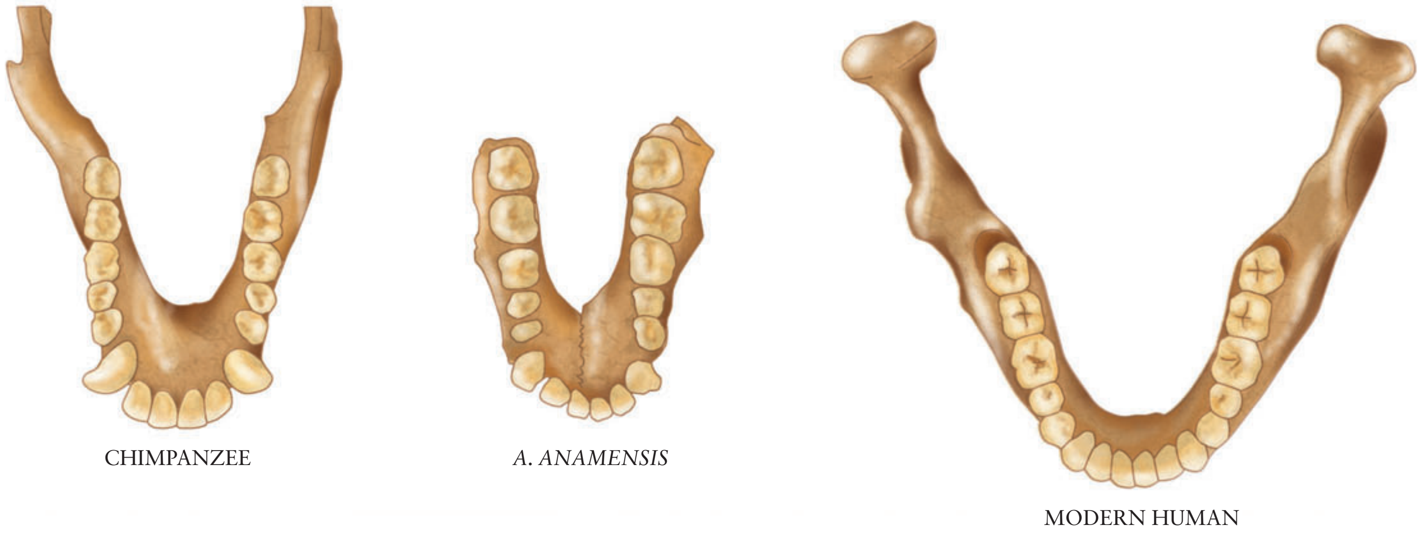


FIGURE 9.16 ■ ***Australopithecus anamensis***
Humans' mandible widens at the rear, causing the two rows of teeth to not be parallel to each other. By contrast, this australopithecine's mandible is like that of apes, U-shaped and with two parallel rows of teeth. Primitive features like this, combined with numerous hominid features, have led many researchers to conclude that *A. anamensis* is the earliest australopithecine.

where the fossils were found in Ethiopia). This hominid is the best-known australopithecine and is represented by hundreds of fossils from dozens of individuals, dating to 3.6–3.0 mya. The most spectacular of the *A. afarensis* fossils—discovered and described by the American paleoanthropologists Donald Johanson, Maurice Taieb, and Tim White—was a 40% complete adult skeleton, nicknamed **"Lucy"** after the Beatles' song "Lucy in the Sky with Diamonds." Recently, in Dikika, the partial skeleton of a three-year-old child was uncovered (**Figure 9.17**).

Especially important about *A. afarensis* is the remarkable representation of Lucy's postcranial skeleton, which includes both arms, much of the pelvis, a left femur and a right tibia, and hand and foot bones. The postcranial skeleton is primitive. Although she was an adept biped, her form of bipedalism differed from modern humans'. That is, her legs are short relative to the lengths of both the body trunk and the arms, and these shorter legs would have produced a somewhat shorter stride length than modern people's. The early hominids probably were striders, but perhaps with less skill than the longer-legged later hominids had. Lucy's arms are about the same as living humans' in the ratio of length to body size. Her fingers are the same length as modern humans', but the phalanges are curved, like pre-australopithecines'. The curvature suggests potential arboreal locomotion using the hands (**Figure 9.18**).

A. afarensis's skull is known from many fragments and teeth, as well as a child's skull and a nearly complete cranium, the latter found in the early 1990s at Hadar by Donald Johanson (**Figure 9.19**). The cranial capacity of this creature and others from the taxon is about 430 cc, that of a small brain, the size of an ape's. The hyoid

Lucy One of the most significant fossils: the 40% complete skeleton of an adult female *A. afarensis,* found in East Africa.

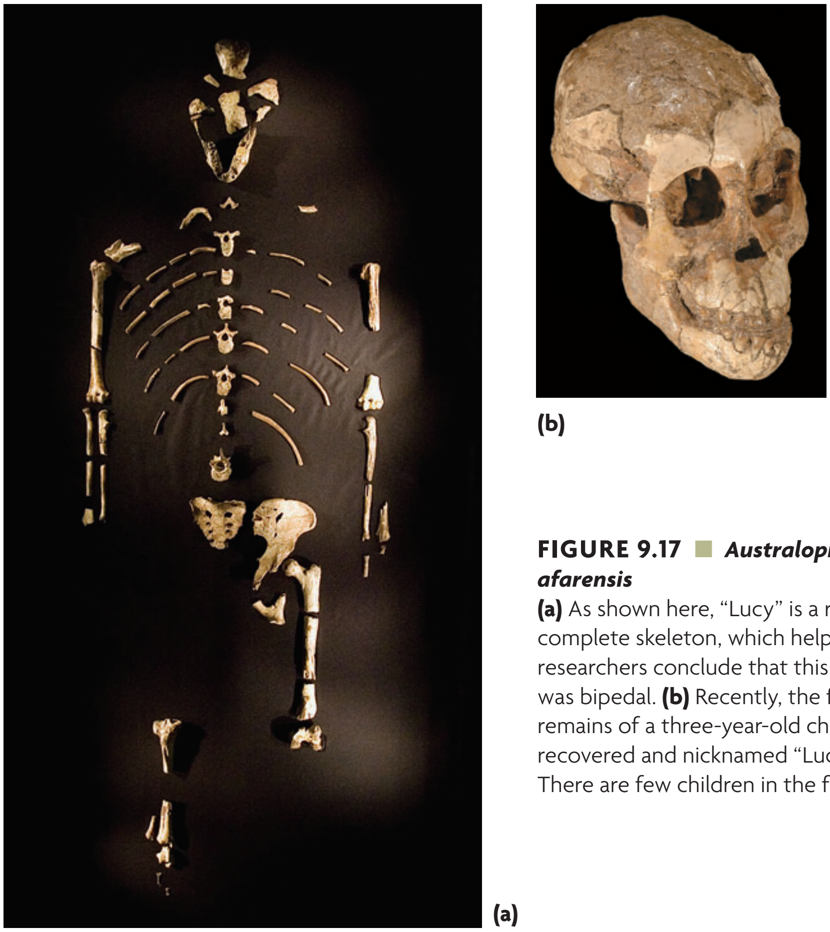


FIGURE 9.17 ■ ***Australopithecus afarensis***
(a) As shown here, "Lucy" is a relatively complete skeleton, which helped researchers conclude that this species was bipedal. **(b)** Recently, the fossil remains of a three-year-old child were recovered and nicknamed "Lucy's baby." There are few children in the fossil record.

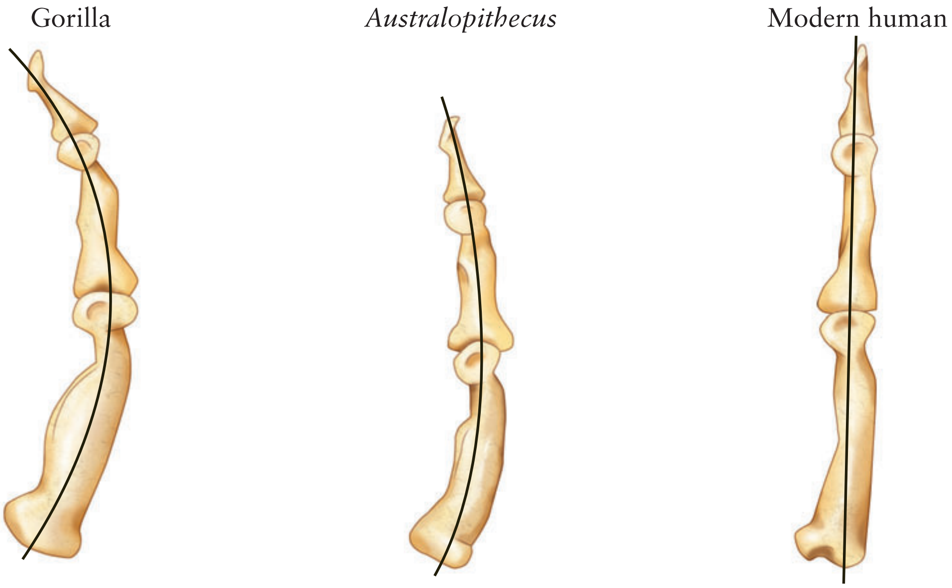


FIGURE 9.18 ■ **Finger and Toe Curvature**
Gorillas and other nonhuman primates have curved phalanges, which provide a better grip on tree branches and improve arboreal locomotion. In modern humans, this curvature has been lost in the hands and feet, as humans are adapted to life on the ground. The phalanges of early hominids, including Australopithecines, have an intermediate amount of curvature, which likely reflects an increasing adaptation to bipedalism but a retained ability to move through the trees.

bone of the child's neck is very much like an ape's. The apelike characteristics of the bone associated with speech indicates the strong likelihood that this hominid did not have speech. The canines are large in comparison with later hominids', the face below the nose projects like an ape's, and overall it looks primitive.

Its many similarities with *A. anamensis* indicate an ancestral-descendant link between the two. *A. afarensis* is not as primitive as the earlier hominid in that the two cusps of the lower third premolars are more equal in size. Moreover, *A. afarensis*'s canines are smaller than the earlier species', and the upper tooth rows are parabolic and not parallel—in other words, more like humans' than like apes'. *A. afarensis*'s mandibles are larger, perhaps reflecting an increased use of the jaws in chewing.

Of the two key *A. afarensis* sites, Laetoli is especially extraordinary because of its assemblage of fossil hominids and because of its spectacular preservation of thousands of footprints left by numerous species of animals, ranging from tiny insects to giant elephants. Geologic evidence indicates the eruption of a nearby volcano, which spewed a thin layer of very fine ash across the landscape. Soon after the eruption, a light rain fell, causing the ash to turn into a thin, gooey layer of mud. Animals then traversed the landscape, among them three hominids that left tracks indicating they had simultaneously walked across the muddy terrain around 3.6 mya (**Figure 9.20**). The footprints are remarkable for having been preserved for millions of years and with such clarity, a preservation made possible because the volcanic ash was wet carbonatite, which dries into a rock-hard substance. Physical anthropologists' study of these tracks reveals that the creatures were humanlike and had three key characteristics of bipedalism: round heels, double arches (front-to-back and side-to-side), and nondivergent big toes.

In contrast to earlier hominids, who were mostly associated with some type of forested environment, *A. afarensis* lived in various habitats, including forests, woodlands, and open country. These diverse environments indicate that hominids

FIGURE 9.19 ■ ***Australopithecus afarensis*** **Cranium**
Although this species was bipedal, its brain size and canine size are more primitive and apelike. Other features of the dentition, however, are more hominidlike, illustrating the creature's intermediate position between the pre-australopithecines and other, later australopithecines.

FIGURE 9.20 ■ **Laetoli Footprints**
These footprints, found in Tanzania, resolved any doubt as to whether *A. afarensis* was bipedal. The tracks were made by three bipedal hominids, two adults and a child who walked in the footprints of one of the adults. In addition to the hominid footprints, many other prints were found at the site, including those of large animals, such as elephants and giraffes, and those of small animals, including rabbits and birds.

became more successful at this time, especially after 4 mya, in adapting to and exploiting new habitats. That *A. afarensis*'s tooth wear is more varied than that of earlier australopithecines indicates that *A. afarensis* probably had a more diverse diet than its predecessors did.

AUSTRALOPITHECUS (KENYANTHROPUS) PLATYOPS **(3.5 MYA)** *Australopithecus* (or ***Kenyanthropus***) *platyops* is a lesser-known hominid from about the same time as *A. afarensis* (**Figure 9.21**). It was discovered by Meave Leakey and her colleagues, at Lomekwi, on the western side of Kenya's Lake Turkana, in deposits that date to about 3.5 mya. Its habitat was mainly woodlands. Its face was unusually flat (*platyops,* from the Greek, means "flat face"), a derived feature in hominids, but still retained some primitive characteristics.

Prior to that time, there had never been more than one hominid species. With the emergence of two contemporary australopithecine taxa, human evolution became more complex. This increasing complexity was related to the beginning of two adaptive patterns—evolutionary lineages—within human evolution.

Diversification of the Hominidae: Emergence of Two Evolutionary Lineages from One (3–1 mya)

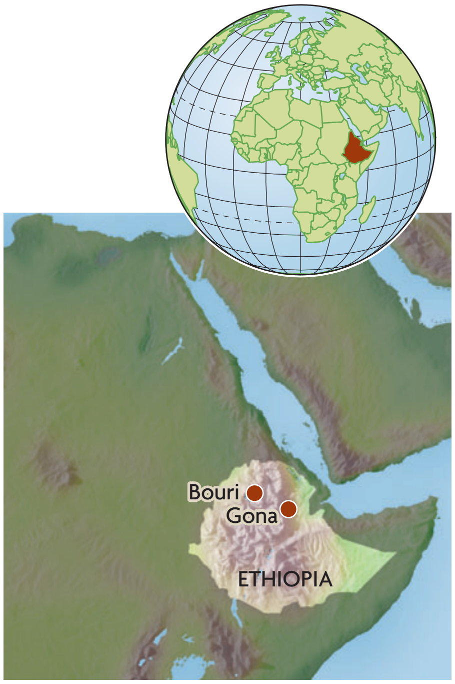
Beginning more than 3 mya, two lineages of hominid evolution began to emerge from one. These two lineages likely reflect two different adaptations. One adaptive pattern is associated with the origin and evolution of the genus *Homo*. The other is represented by descendants of *A. afarensis*, leading to the evolution of two later australopithecine lineages, one in East Africa and the other in South Africa. The

FIGURE 9.21 ■ ***Australopithecus (Kenyanthropus) platyops***
A contemporary of *A. afarensis,* this australopithecine was unique in having a flat face and small teeth. Its brain size, however, was similar to that of *A. afarensis.*

lineage leading to *Homo* survives to the present, whereas the australopithecine lineages became extinct by about 1 mya (**Figure 9.22**). Here, we look at the two emerging forms of early hominids.

AUSTRALOPITHECUS GARHI (2.5 MYA): THE FIRST MAKER, AND USER, OF TOOLS Soon after discovering *A. afarensis* at Hadar, Johanson and White began to suspect that *A. afarensis* was the most likely ancestor of the genus *Homo*. However, the ancestral-descendant linkage between the two taxa was difficult to identify, owing to the virtual lack of a hominid fossil record in East Africa dating to 3–2 mya, the time during which earliest *Homo* likely evolved (discussed further in chapter 10). In 1999, this picture changed dramatically, when the Ethiopian paleoanthropologist Berhane Asfaw and his associates discovered a new *Australopithecus* species, which they named ***Australopithecus garhi*** (*garhi* means "surprise" in the Afar language). Found in Bouri, in Ethiopia's Middle Awash region, it dated to about 2.5 mya.

A. garhi is represented by bones, teeth, a partial skeleton, and a skull (**Figure 9.23**). Its teeth were larger than the earlier australopithecines'. Its third premolar's two cusps were almost equal in size. As in *A. afarensis,* beneath the nose the face had a primitive projection, and the brain was small (450 cc). For the first time in hominid evolution, the ratio of arm (humerus) length to leg (femur) length was much more humanlike than apelike, resulting from the femur's lengthening. This more humanlike ratio indicates a decreased commitment to the arborealism of earlier australopithecines. These features combined—especially the chronological position at 2.5 mya and the cranial, dental, and postcranial features—suggest that *A. garhi* was ancestral to *Homo*. Environmental reconstructions based on animal remains and other evidence indicate that this hominid lived on a lakeshore, as was typical of later australopithecines and early *Homo*.



At least one or both early hominids made and used stone tools. Paleoanthropologists have found very primitive stone tools from a number of sites in East Africa dating to the late Pliocene, 2.5–2.0 mya. These stone tools are part of the **Oldowan Complex,** the first hominid culture and the earliest culture of the **Lower Paleolithic,** named by Louis and Mary Leakey from their work at Olduvai Gorge. The Leakeys concluded that these crude stone tools must have been produced by the larger-brained early *Homo* found at the site, rather than by the contemporary smaller-brained australopithecines. Although no tools have been found at Bouri, the Belgian paleoanthropologist Jean de Heinzelin, the American anthropologist Desmond Clark, and their colleagues found mammal bones at the site having distinctive cutmarks and percussion marks that were produced by stone tools. This evidence indicates that *A. garhi* used stone tools to process animal remains for food (**Figure 9.24**). At the Gona River site, in the Middle Awash region, actual tools—the earliest known—have been found dating to around 2.6 mya. Though extraordinarily primitive, the tools would have been effective at cutting (**Figure 9.25**).

Archaeologists have long assumed that such primitive tools were used for cutting animal tissues to obtain the meat. Stone tools may indeed have been used this way. However, bone tools found in some South African caves show distinctively polished patterns of microscopic wear. Through experiments, the South African paleoanthropologist Lucinda Backwell and the French paleoanthropologist Francesco d'Errico have shown this kind of wear to be produced by digging in the ground, especially digging in termite mounds. Their finding supports the idea that early hominids ate insects (in addition to meat). While the idea of eating insects is

Australopithecus garhi A late australopithecine from East Africa that was contemporaneous with *A. africanus* and *A. aethiopicus* and was the likely ancestor to the *Homo* lineage.

Oldowan Complex The stone tool culture associated with *H. habilis* and, possibly, *A. garhi,* including primitive chopper tools.

Lower Paleolithic The oldest part of the period during which the first stone tools were created and used, beginning with the Oldowan Complex.

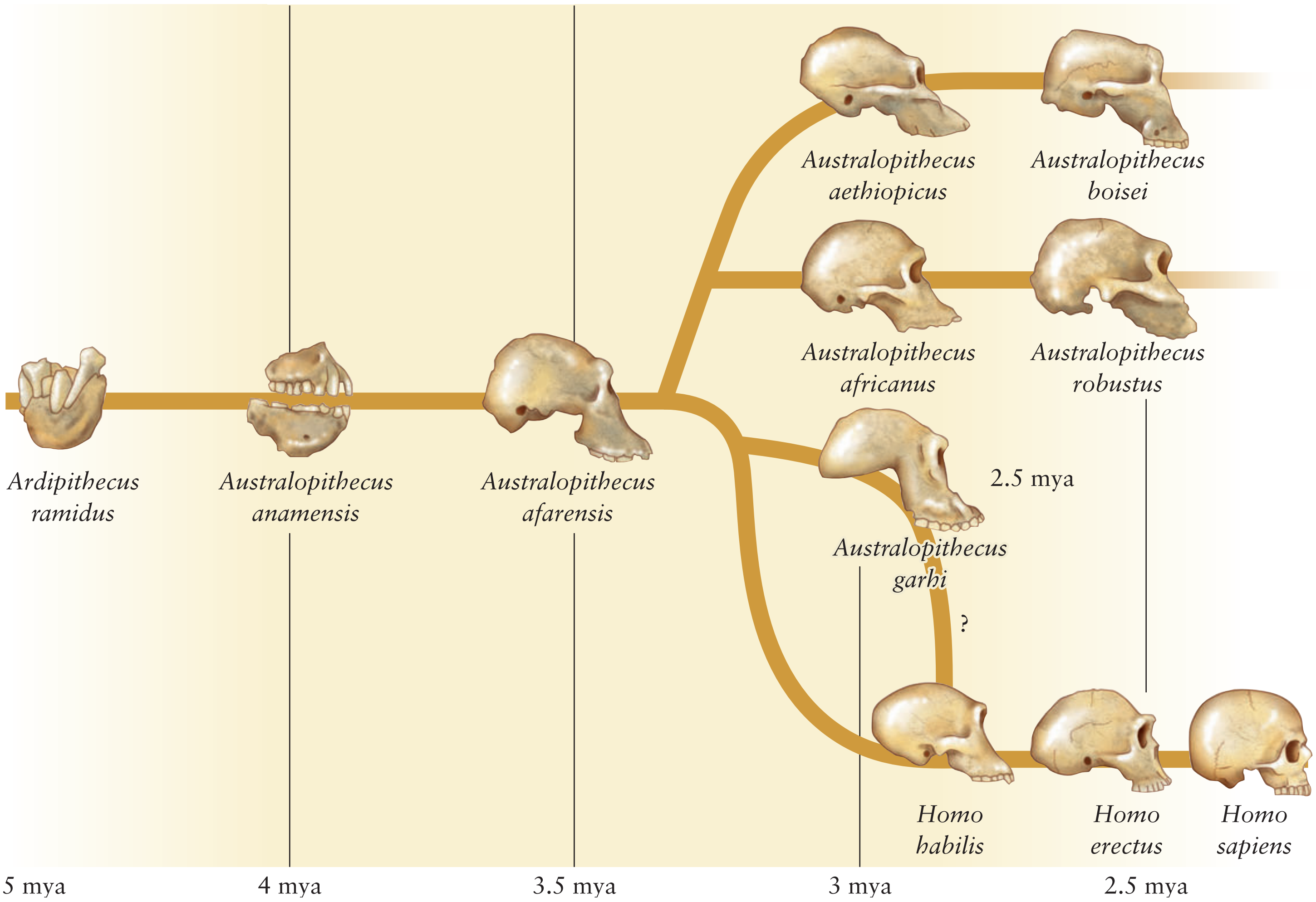


FIGURE 9.22 ■ **Hominid Lineages**
The evolutionary relationships among the various *Australopithecus* species suggest two main lineages: one leading to modern *Homo sapiens* and the other leading to a number of australopithecines. (This second lineage is shown here as two separate lines, one from East Africa and the other from South Africa.) The ancestor to both lineages is hypothesized to be *A. afarensis,* which may be a descendant of *Ardipithecus* and *A. anamensis.* (Fossil credit: *Ardipithecus ramidus* and *Australopithecus garhi*, Middle Awash Research Project, redrawn from photographs © David L. Brill.)

revolting to our Western tastes, insects would have provided important proteins for our ancestors. Alternatively, the bone tools may have been used for digging up edible roots.

Unlike Olduvai Gorge and other, younger sites where *Australopithecus* and early *Homo* were found in the same general locality, Bouri has not yielded remains of early *Homo*. In all likelihood, *Homo* had not yet evolved in East Africa, indicating that *Australopithecus* was perhaps the first hominid to produce and use stone tools. These tools were used both to butcher animals for food and for other functions. Tool use might also have begun before 2.6 mya. Evidence of earlier tool use might not have been found because tools had been made—and probably were made—out of more ephemeral materials, such as wood and grass. In the kinds of environments

FIGURE 9.23 ■ ***Australopithecus garhi***
This "surprise" hominid may be the link between *A. afarensis* and the *Homo* genus. That some of its traits are similar to those of *A. afarensis* while others are similar to features of *Homo* suggests its intermediate status. (Photograph © 1999 David L. Brill.)

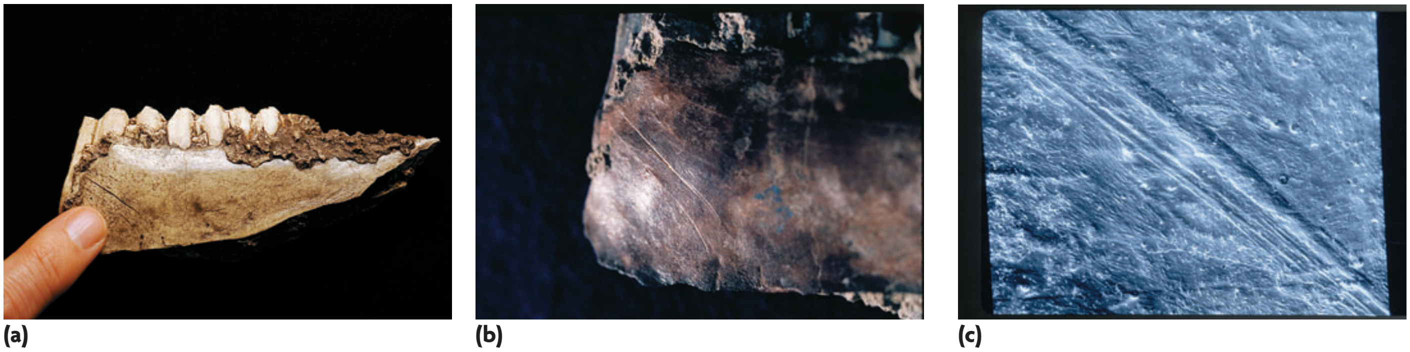


FIGURE 9.24 ■ **Tool Use and *A. garhi***
(a–c) Particular cutmarks on animal remains suggest that *A. garhi* used stone tools. The marks on this bovid mandible may have been made when the tongue was removed.

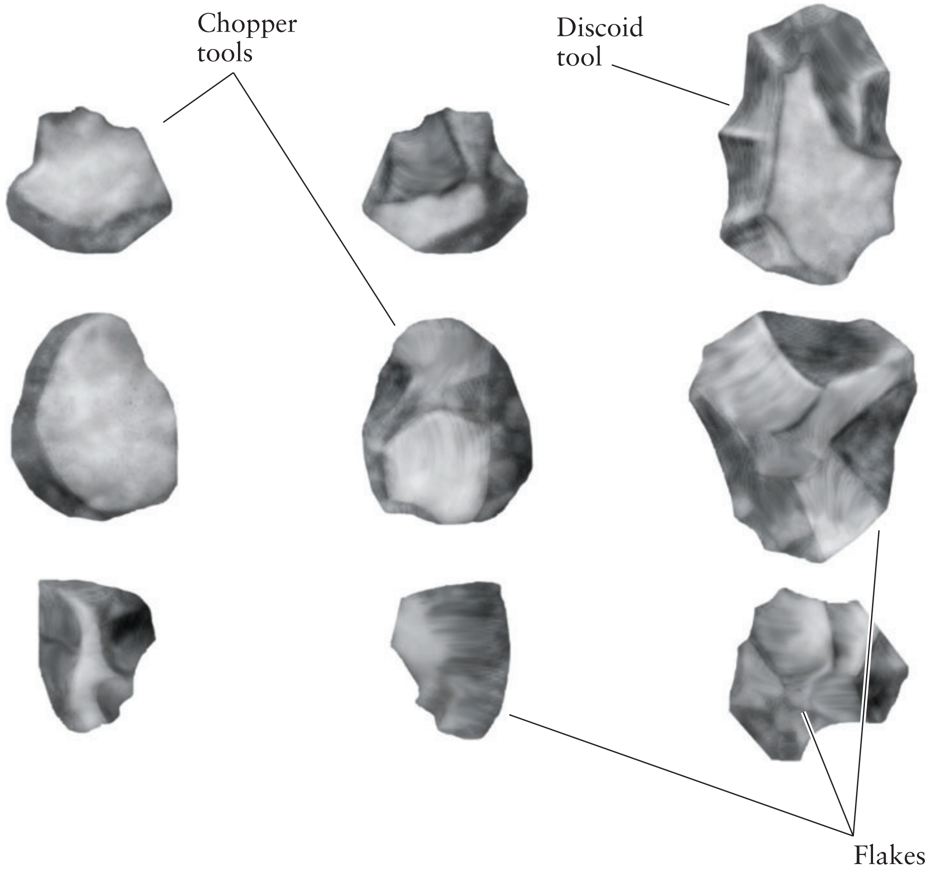


FIGURE 9.25 ■ **Oldest Stone Tools**
A number of stone tools, known as Oldowan tools, were uncovered in the Middle Awash Valley. These primitive tools were not found in association with hominid remains, so it is unclear which genera or species produced them. Among the remains were flaked pieces and "chopper" tools; these may have had various functions.

in which the earliest hominids lived, these materials would not have survived. Other evidence suggests, though, that hominids living before 2.6 mya used tools. For example, australopithecines' hand bones have anatomical features associated with finer manipulation than that used by living apes. The paleoanthropologist Randall Susman has found evidence of a flexor muscle in australopithecines' thumb, very similar to a muscle in living humans that is absent in apes. The flexor muscle makes possible the finer precision use of the thumb and other fingers for tool production and tool use.

Evolution and Extinction of the Australopithecines

In addition to *A. garhi,* other australopithecine species lived in East Africa and South Africa. In East Africa, the species included earlier and later forms of robust australopithecines called ***Australopithecus aethiopicus*** (named for Ethiopia, the country where they were first found) and ***Australopithecus boisei*** (named for a benefactor who supported the discoverer's research), respectively. The earlier hominid, from the west side of Lake Turkana, dates to about 2.5 mya and had a brain size of about 410 cc. The later hominid, from Olduvai Gorge and around Lake Turkana, dates to 2.3–1.2 mya and had a brain size of about 510 cc. Compared with earlier australopithecines, these robust australopithecines had smaller front teeth, larger back teeth, and larger faces. Their most visually striking characteristic was a massive attachment area, on the skull, for the temporalis muscle, resulting in a well-developed sagittal crest. Both their premolars and their molars were enormous. These big teeth with large chewing surfaces, combined with large chewing muscles, made robust australopithecines the ultimate grinders (**Figure 9.26**).

Australopithecus aethiopicus An early robust australopithecine from East Africa, with the hallmark physical traits of large teeth, large face, and massive muscle attachments on the cranium.

Australopithecus boisei Formerly known as Zinjanthropus boisei; a later robust australopithecine from East Africa that was contemporaneous with *A. robustus* and *A. africanus* and had the robust cranial traits, including large teeth, large face, and heavy muscle attachments.

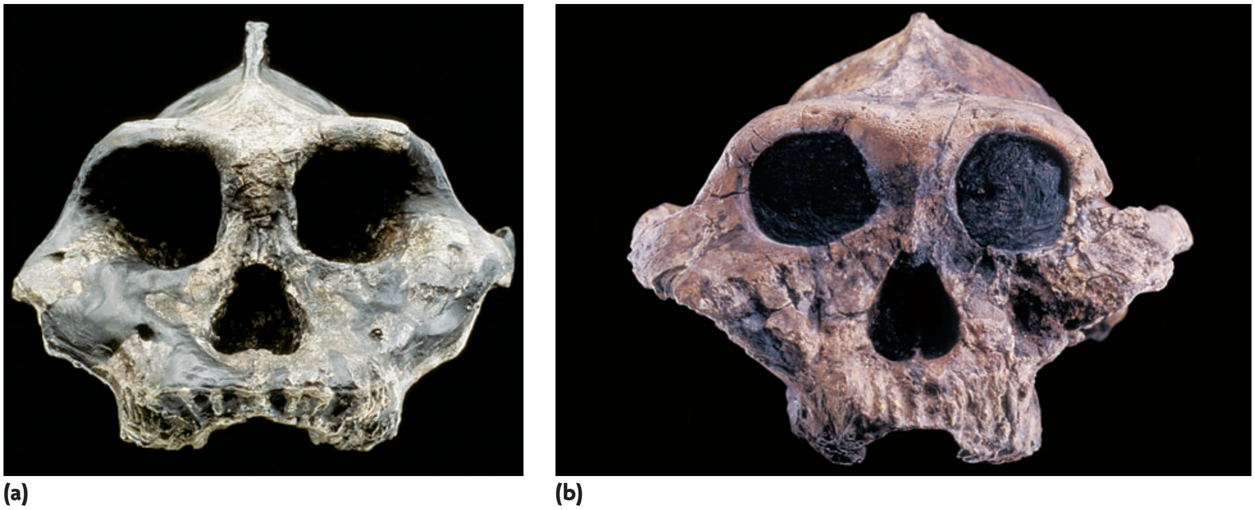


FIGURE 9.26 ■ **Robust Australopithecines**
(a) *Australopithecus aethiopicus* and **(b)** *Australopithecus boisei* had a large sagittal crest; large, flaring zygomatic, or cheek, bones; and large teeth. The description of these australopithecines as robust, however, applies only to their crania and is likely related to a diet rich in hard foods. Neither of these bipedal species had a robust postcranial skeleton. (Photographs [a] © 1995 David L. Brill and [b] © 1985 David L. Brill.)

Australopithecines' increasing cranial robusticity after about 2.5 mya indicates that they were increasingly focused on acquiring and eating foods that required more powerful chewing muscles than before. That is, they were eating harder foods. Robust australopithecines' presence in East Africa ended sometime before 1 mya, indicating that they became extinct at about that time.

In South Africa, a very similar trend of increasing cranial and dental robusticity began 3–2 mya. These changes coincided with a shift in habitat from forest to grasslands around 2.5 mya. At the Taung site in 1925, the Australian anthropologist Raymond Dart was the first to describe the earliest evidence of hominids in South Africa, a species he named ***Australopithecus africanus*** (**Figure 9.27**). Found also in Sterkfontein and Makapansgat, *A. africanus* dates to about 3–2 mya and had larger teeth than those of *A. afarensis* (**Figure 9.28**). After about 2 mya, a descendant species, ***Australopithecus robustus*** (sometimes called *Paranthropus robustus*) arose, and it is represented by fossils from Swartkrans, Kromdraai, and Drimolen.

Australopithecus africanus A gracile australopithecine from South Africa that was contemporaneous with *A. aethiopicus, A. garhi,* and *A. boisei* and was likely ancestral to *A. robustus.*

Australopithecus robustus A robust australopithecine from South Africa that may have descended from *A. afarensis,* was contemporaneous with *A. boisei,* and had the robust cranial traits of large teeth, large face, and heavy muscle attachments.

South Africa's youngest-dating australopithecines had large premolars, large molars, big faces, and well-developed sagittal crests—these hominids were similar in many respects to their East African counterparts (**Figure 9.29**). Australopithecines' increasing robusticity in South Africa and East Africa indicates a widespread adaptation involving an increased focus on foods that required heavy chewing. Moreover, *A. robustus*'s teeth had more pits on the chewing surfaces and thicker enamel than *A. africanus*'s teeth, indicating that the later australopithecines specialized in eating harder food, such as hard fruits and seeds.

As in East Africa, the australopithecines in South Africa went extinct by 1 mya. The reasons for this extinction are unclear. However, the lineage leading to *Homo*

FIGURE 9.27 ■ **Taung, South Africa**
Some of the earliest evidence of hominids in South Africa was discovered in a limestone quarry in Taung. For some time, the species found there, *A. africanus,* overlapped temporally with *A. afarensis,* of East Africa. In addition, the small, gracile species had a number of humanlike features.

FIGURE 9.28 ■ ***Australopithecus africanus***
This *Australopithecus africanus* cranium was discovered in a series of limestone caves known as Sterkfontein. Located in South Africa, this site has been declared a UNESCO World Heritage Site. Unlike the robust australopithecines also discovered in South Africa, this *A. africanus* cranium is gracile.

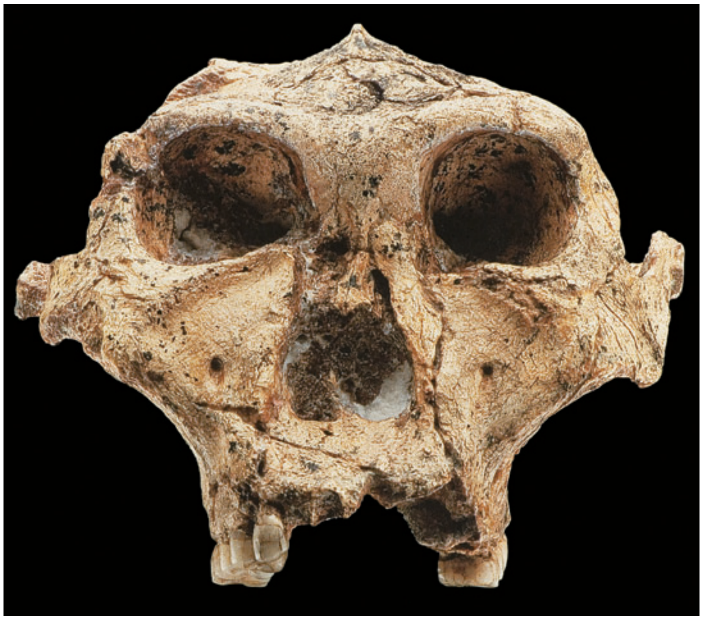


FIGURE 9.29 ■ ***Australopithecus robustus***
Also discovered in South Africa, this robust australopithecine shares many traits with East Africa's robust species. One of these traits, dietary specialization, might have led to the eventual extinction of both *A. robustus* and the East African robust species, as they were not able to adapt to vegetation changes caused by climate change.

seems to have developed an increasingly flexible and generalized diet, whereas the later robust australopithecines' diets became less flexible and more specialized. This increasing focus on a narrower range of foods in the later robust australopithecines may have led to their extinction. Their brains show very little increase in size. The brains of South African *A. africanus* and *A. robustus* were only about 450 cc and 530 cc, respectively.

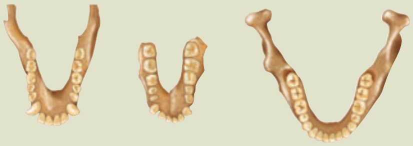
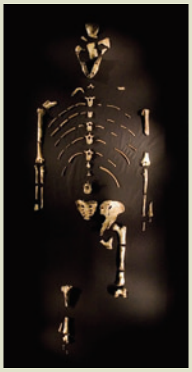
From the late Miocene through the Pliocene and into the Pleistocene—about 6–1 mya—the earliest hominids began to evolve. These diverse hominids had increasingly specialized diets, and their cranial morphology reflected this specialization. They experienced no appreciable change in brain size or body size, however. Thus, evolution focused on mastication. A new genus of and species of hominid, ***Homo habilis***—having a larger brain and reduced chewing complex—made its appearance (**Table 9.2**). At that time, australopithecines were diverse, evolving, and a significant presence on the African landscape. This gracile hominid likely evolved from an australopithecine, and the ancestor may have been *A. garhi*. This point in human evolution is critically important because it is the earliest record of a remarkable adaptive radiation, leading to the most prolific and widespread species of primate: us.

Homo habilis The earliest *Homo* species, a possible descendant of *A. garhi* and an ancestor to *H. erectus*; showed the first substantial increase in brain size and was the first species definitively associated with the production and use of stone tools.

CONCEPT CHECK

The Australopithecines

The australopithecines existed about 4–1 mya. Their fossils are from East Africa and South Africa. These creatures were still primitive in a number of ways, but they were more humanlike than apelike compared with the pre-australopithecines.

HOMINID	DATE(S)	LOCATION(S)
Australopithecus anamensis	4 mya	Lake Turkana, Kenya Awash River Valley, Ethiopia
 Key features: Skull fragments, teeth, postcrania found Large outer cusp (like apes') on third premolar Large canines Parallel tooth rows in upper jaw (like apes') Curved hand phalanx Less than 1 m (4 ft) tall Lived in wooded setting		
Australopithecus afarensis	3.6–3.0 mya	Hadar, Ethiopia
 Key features: Skulls, teeth, postcrania (hundreds of pieces) found Partial adult skeleton (Lucy) Partial juvenile (three-year-old) skeleton Small brain (430 cc) Hyoid like apes' Mandible larger in earlier Laetoli than in later Hadar Smaller canines than in earlier species Equal-size cusps on third premolar (like humans') Parabolic tooth rows in upper jaw Curved hand phalanges Short legs Footprints indicate bipedal foot pattern Lived in wooded setting, but a more open one than associated with *Ardipithecus* or *A. anamensis*		
Australopithecus platyops	3.5 mya	Lomekwi, Kenya
 Key features: Skull and teeth found Flat face Small brain (400–500 cc) Contemporary with *A. afarensis,* signaling split of australopithecine lineage into two Lived in woodlands		
Australopithecus africanus	3.0–2.0 mya	Taung, South Africa Sterkfontein, South Africa Makapansgat, South Africa
 Key features: Skulls, teeth, endocast (impression of brain), postcrania, two partial adult skeletons found Small brain (450 cc) Moderate-size teeth Equal-size cusps on third premolar Phalanges not curved Adult partial skeleton has apelike leg-to-arm ratio (short legs, long arms) Lived in open grasslands		

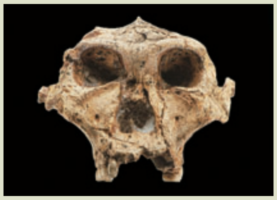
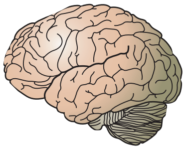
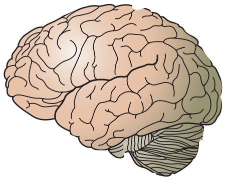
HOMINID	DATE(S)	LOCATION(S)
Australopithecus garhi  Key features: Skull, teeth, postcrania found Small brain (450 cc) Equal-size cusps on third premolar Teeth larger than in earlier *A. afarensis* Ratio of upper arm length to upper leg length more humanlike than apelike Curved foot phalanx (like *A. afarensis*'s) Lived in grasslands, on lakeshore Tool maker/user (animal butchering)	2.5 mya	Bouri, Ethiopia
Australopithecus boisei  Key features: Skull and teeth found Small brain (510 cc) Massive posterior teeth Rubust skull with sagittal crest Lived in open grasslands	2.3–1.2 mya	Olduvai, Tanzania Lake Turkana, Kenya
Australopithecus aethiopicus  Key features: Skull and teeth found Small brain (410 cc) Massive posterior teeth Robust skull with sagittal crest Lived in open grasslands	2.5 mya	Lake Turkana, Kenya
Australopithecus robustus  Key features: Skull and teeth found Small brain (530 cc) Massive posterior teeth Robust skull with sagittal crest Lived in open grasslands	2.0–1.5 mya	Swartkrans, South Africa Kromdraai, South Africa Drimolen, South Africa

TABLE 9.2 Trends from Late Australopithecine to Early *Homo*

	LATE AUSTRALOPITHECINE	→	EARLY *HOMO*
Brain		Increase in size	
Face		Reduction in size	
Teeth		Reduction in size	

ANSWERING THE **BIG** QUESTIONS

What is a hominid?

- Hominids are defined by two obligate behaviors: bipedal locomotion and nonhoning chewing.

Why did hominids evolve from an apelike primate?

- The Hominidae's origin is closely tied to the origins of bipedal locomotion. This form of movement may have provided early hominids with a more efficient means of exploiting patchy forests, freeing the hands for feeding in trees and on the ground.

Who were the first hominids?

- The earliest fossil hominids were the pre-australopithecines, dating to 7–4 mya. These hominids lived in forests.
- The pre-australopithecines gave rise to the australopithecines, dating to 4–1 mya.

What was the evolutionary fate of the first hominids?

- The evolution of the australopithecine lineages resulted in generally increased robusticity of the chewing complex, no change in brain size, and eventual extinction. The change in the chewing complex reflected an increasing emphasis on eating hard foods, especially plants.
- By 2.5 mya, at least one australopithecine lineage gave rise to the genus *Homo*. Having evolved from earlier australopithecines, at least two other australopithecine lineages, one in East Africa and one in South Africa, went extinct around 1 mya.

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KEY TERMS

Ardipithecus kadabba
Ardipithecus ramidus
Australopithecus aethiopicus
Australopithecus afarensis
Australopithecus africanus
Australopithecus anamensis
Australopithecus boisei
Australopithecus garhi
Australopithecus (or *Kenyanthropus*) *platyops*
Australopithecus robustus
Eoanthropus dawsoni
Homo habilis
Lower Paleolithic
Lucy
Oldowan Complex
Orrorin tugenensis
Sahelanthropus tchadensis

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